

EXISTENCE OF TRAVELLING PULSES IN A NEURAL MODEL

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This paper is dedicated to the memory of J. Bryce McLeod, 1929-2014, a dear friend and inspiring collaborator.

ABSTRACT. In 1992 G. B. Ermentrout and J. B. McLeod published a landmark study of travelling wavefronts for a differential-integral equation model of a neural network. Since then a number of authors have extended the model by adding an additional equation for a “recovery variable”, thus allowing the possibility of travelling pulse type solutions. In a recent paper G. Faye gave perhaps the first rigorous proof of the existence (and stability) of a travelling pulse solution for a model of this type, treating a simplified version of equations originally developed by Kilpatrick and Bressloff. The excitatory weight function J used in this work allowed the system to be reduced to a set of four coupled ODEs, and a specific firing rate function S , with parameters, was considered. The method of geometric singular perturbation was employed, together with blow-ups. In this paper we extend Faye’s results on existence by dropping one of his key hypotheses, proving the existence of pulses at at least two different speeds, and in a sense, allowing a wider range of the small parameter in the problem. The proofs are classical, and self-contained aside from standard ode material.

1. INTRODUCTION

In this paper we consider the following system of equations:

$$(1.1) \quad \begin{aligned} \frac{\partial u(x,t)}{\partial t} &= -u(x,t) + \int_{-\infty}^{\infty} J(x-y) q(y,t) S(u(y,t)) dy \\ \frac{1}{\varepsilon} \frac{\partial q(x,t)}{\partial t} &= 1 - q(x,t) - \beta q(x,t) S(u(x,t)) \end{aligned} ,$$

where J is a normalized exponential

$$(1.2) \quad J(x) = \frac{b}{2} e^{-b|x|}$$

and the “firing rate” function S is given by

$$(1.3) \quad S(u) = \frac{1}{1 + e^{\lambda(\kappa - u)}},$$

for certain positive parameters ε , λ , b , κ , and β . The variable u is the synaptic input current for a neural network with synaptic depression, the effect of which is represented by the scaling factor q . These equations were proposed and studied by G. Faye in [4].

The Faye model is a simplified version of one first introduced by Kilpatrick and Bressloff in [14]. These authors included a variable and equation to allow for spike frequency adaptation. However they show by numerical computation that adaptation has little effect on the resulting waves. Faye dropped the adaptation equation and variable in [14] to get his system (1.1). See [4] and [14] for further information on the physical background of (1.1).

In [4] the author proves two interesting results about the system (1.1), namely the existence of a “travelling pulse” solution and the stability of this solution. A travelling pulse solution of (1.1) is a non-constant solution (u, q) of the form

$$(u(x + ct), q(x + ct))$$

such that both $\lim_{s \rightarrow \infty} (u(s), q(s))$ and $\lim_{s \rightarrow -\infty} (u(s), q(s))$ exist and these limits are equal. In this paper we are interested in the existence of values of c for which (1.1) has such a solution. As we describe briefly below, using (1.2) leads to a set of four ode’s in which c is a parameter. To show that a travelling pulse exists for some $c > 0$, Faye uses the theory of geometric singular perturbation initiated by Fenichel in [6] and extended by Jones and Kopell in [13]. The “blowup” method is also employed [2].

Here we extend the existence result in [4] in several ways. We show that for sufficiently small $\varepsilon > 0$ there are at least two travelling pulses, hence a “fast” pulse and a “slow” pulse, for speeds $c^* > c_* > 0$. Also, we remove an important hypothesis used in [4], one which can only be verified by numerical integration of a related ode system. (This hypothesis is stated and discussed in Section 4.) Our proof is for a general class of firing functions which includes the specific S for which Faye states his theorem.

Further, we use a method which allows, in some sense, a larger range of ε than seems possible with geometric perturbation. This will be made precise in the statements of our theorems. We believe, based on our past experience with a similar problem, that it is feasible to check existence rigorously for particular positive values of $\varepsilon > 0$, using precise numerical analysis based on interval arithmetic, but we have not carried out such a check. This will be explained further in Section 4.

We now mention two well-known predecessors of the Kilpatrick-Bressloff and Faye models. In 1992, Ermentrout and McLeod studied the equation

$$(1.4) \quad u_t = -u + \int_{-\infty}^{\infty} J(x - y) S(u(t, y)) dy.$$

As above, S is positive, bounded, and increasing. Since there is no feedback in the equation, (1.4) supports only traveling fronts, where u is monotone. In the landmark paper [3] Ermentrout and McLeod proved the existence of fronts for a wide variety of symmetric positive weight functions J and firing rates S . (Their work applied to a more general equation) Subsequently, in [16], Pinto and Ermentrout introduced the needed negative feedback in order to get pulses. Their system is

$$(1.5) \quad \begin{aligned} \frac{\partial u(x, t)}{\partial t} &= -u - v + \int_{-\infty}^{\infty} J(x - y) S(u(t, y)) dy \\ \frac{1}{\varepsilon} \frac{\partial v(x, t)}{\partial t} &= u - \gamma v \end{aligned} .$$

They analyzed this system primarily for the case $S(u) = H(u - \kappa)$ where H is the Heaviside function and κ is a constant representing a firing threshold. While some partial results have been obtained recently by Scheel and Faye (see Section 4), we are not aware of any existence proof for pulses which covers all reasonable smooth functions S . We discuss what we mean by “reasonable” in Section 4, where we also indicate why our method does not appear to apply to this model, and why

we expect that (1.5) supports a richer family of bounded traveling waves than exist for (1.1).¹

2. STATEMENT OF RESULTS

Travelling pulse solutions of (1.1) with (1.2) are shown to satisfy a system of ode's by letting $v(s) = \int_{-\infty}^{\infty} \frac{b}{2} e^{-b|s-\tau|} q(\tau) J(u(\tau)) d\tau$ and computing $w = v'$ and w' .² We find that

$$(2.1) \quad \begin{aligned} u' &= \frac{v-u}{c} \\ v' &= w \\ w' &= b^2(v - qS(u)) \\ q' &= \frac{\varepsilon}{c}(1 - q - \beta qS(u)). \end{aligned}$$

We will denote solutions of this system by $p = (u, v, w, q)$, and we look for values of c for which there is a non-constant solution p such that $p(\infty)$ and $p(-\infty)$ both exist and are equal. The orbit of such a solution of (2.1) is called “homoclinic”. In the language of dynamical systems, $(u(x+ct), q(x+ct))$ is a pulse solution of (1.1) if and only if the orbit of p is homoclinic.

We make the following assumptions on S .

Condition 1. *The function S is positive, increasing, bounded, and has a continuous first derivative S' .*

Condition 2. *The function $h(u) = \frac{u}{S(u)}$ has one local maximum followed by one local minimum, and no other critical points.*

Condition 3. *S is such that the system (2.1) has exactly one equilibrium point, say $p_0 = (u_0, u_0, 0, q_0)$.*

Condition 4. *The function S is also such that the “fast” system*

$$(2.2) \quad \begin{aligned} u' &= \frac{v-u}{c} \\ v' &= w \\ w' &= b^2(v - q_0S(u)) \end{aligned}$$

has three equilibrium points, $(u_0, u_0, 0)$, $(u_m, u_m, 0)$, and $(u_+, u_+, 0)$, with $u_0 < u_m < u_+$.

Condition 5.

$$\int_{u_0}^{u_+} (q_0S(u) - u) du > 0.$$

For convenience we will assume that $0 < S < 1$ on $(-\infty, \infty)$. Then Conditions 1-4 imply that $0 < q_0 < 1$, $u_0 > 0$, and $u_+ < 1$.

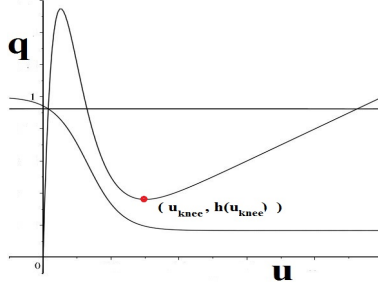
We will denote solutions of (2.2) by $r = (u, v, w)$. The local minimum of h will be denoted by u_{knee} . In [4] specific ranges of κ and λ are given so that these conditions are satisfied by the function given in (1.3). In Figure 1 we show the graphs of h , $\frac{1}{1+\beta S}$ (the q nullcline), and $q = q_0$, when S is given by (1.3). We use the same parameter values as were chosen for illustration in [4].³

We can now state our first main result.

¹We thank the anonymous referee, who helped improve the presentation and who asked several questions which should have been answered in the original version.

²It is not necessary to discuss Fourier transforms, as is usually done here.

³ $\lambda = 20$, $\kappa = 0.22$, $\beta = 5$, $b = 4.5$

FIGURE 1. graphs of h , $\frac{1}{1+\beta S}$, and $q = q_0$

Theorem 1. *If Conditions 1- 5 are satisfied, and ε is positive and sufficiently small, then there are at least two positive values of c , say $c^* > c_*$, such that (2.1) has a non-constant solution p satisfying*

$$\lim_{t \rightarrow -\infty} p(t) = \lim_{t \rightarrow \infty} p(t) = p_0.$$

In order to state our remaining theorems it is convenient first to give some basic information about the fast system, (2.2). We state this information as a pair of lemmas, which will be used in proving our Theorems. Their proofs are given in the Appendix.

Lemma 1. *If Conditions 4 and 5 are satisfied, then for each $c > 0$ the equilibrium point $(u_0, u_0, 0)$ of (2.2) is a saddle point, with a one dimensional unstable manifold $\mathcal{U}_{0,c}$ and a two dimensional stable manifold $\mathcal{S}_{0,c}$. There is, for each $c > 0$, a unique solution $r_c = (u_{0,c}, v_{0,c}, w_{0,c})$ of (2.2) with $r_c(t) \in \mathcal{U}_{0,c}$ for all t and satisfying the conditions*

$$(2.3) \quad \begin{aligned} u_{0,c}(0) &= u_m \\ w_{0,c} &> 0 \text{ on } (-\infty, 0]. \end{aligned}$$

Further, there is a unique $c = c_0^* > 0$ such that $w_{0,c_0^*} > 0$ on R and

$$\lim_{t \rightarrow \infty} r_{c_0^*}(t) = (u_+, u_+, 0).$$

In other words, the branch $\mathcal{U}_{0,c_0^*}^+$ of \mathcal{U}_{0,c_0^*} pointing into the positive octant $u > u_0, v > u_0, w > 0$ is a heteroclinic orbit connecting $(u_0, u_0, 0)$ to $(u_+, u_+, 0)$. Also, $w_{0,c_0^*} > 0$ on $(-\infty, \infty)$, which implies that $v'_{0,c_0^*} > 0$ and $u'_{0,c_0^*} > 0$. This solution is called a “front” for (2.2). A front for (2.2) can be characterized as a solution of this equation which exists on $(-\infty, \infty)$, is nonconstant and bounded, and satisfies $u'_c > 0$ on $(-\infty, \infty)$.

Lemma 2. *If $c > c_0^*$ then $w_{0,c} > 0$ on R , and*

$$\lim_{t \rightarrow \infty} u_{0,c}(t) = \lim_{t \rightarrow \infty} v_{0,c}(t) = \infty.$$

If $0 < c < c_0^$ then $w_{0,c}$ is initially positive and has a unique zero. Also, $u'_{0,c}$ has a unique zero, and*

$$\lim_{t \rightarrow \infty} u_{0,c}(t) = \lim_{t \rightarrow \infty} v_{0,c}(t) = -\infty.$$

If $c \in (0, c_0^)$ and $t_1(c)$ is the zero of $u'_{0,c}$, where $u_{0,c}$ is a maximum, then $u''_{0,c}(t_1(c)) < 0$ and $\lim_{c \rightarrow c_0^*-} r_c(t_1(c)) = (u_+, u_+, 0)$.*

Suppose finally that for some $c_1 \in (0, c_0^*)$, $w_{0,c_1} > 0$ on an interval $(-\infty, T(c_1))$, $w_{0,c_1}(T(c_1)) = 0$, and

$$v_{0,c_1}(T(c_1)) > q_0 S(u_{knee}).$$

Then for any $c \in [c_1, c_0^*)$,

$$u_{0,c}(t_1(c)) > u_{knee}.$$

Remark 1. We conjecture that the condition

$$u_{0,c_1}(T(c_1)) > u_{knee}$$

would imply the same conclusion, but we have not been able to prove this.

The positive number c_0^* defined in Lemma 1 plays an important role throughout this paper.

Theorem 2. Suppose that Conditions 1- 5 are satisfied. Suppose also that there is a $c_1 \in (0, c_0^*)$, such that if $T(c_1)$ is the unique zero of w_{0,c_1} (which exists by Lemma 2), then

$$(2.4) \quad v_{0,c_1}(T(c_1)) > q_0 S(u_{knee}).$$

Assume as well that for some $\varepsilon > 0$ there is a solution $p_{\varepsilon,c_1} = (u_{\varepsilon,c_1}, v_{\varepsilon,c_1}, w_{\varepsilon,c_1}, q_{\varepsilon,c_1})$ of (2.1) with $c = c_1$ which has the following properties:

$$(i) \quad \lim_{t \rightarrow -\infty} p_{\varepsilon,c_1}(t) = p_0$$

$$(ii) \quad \begin{cases} u'_{\varepsilon,c_1} > 0 \text{ on some interval } (-\infty, t_1) \text{ and } u''_{\varepsilon,c_1}(t_1) < 0 \\ u'_{\varepsilon,c_1} < 0 \text{ on some interval } (t_1, t_3] \text{ and } u_{\varepsilon,c_1}(t_3) = 0 \end{cases}$$

Then for the given ε there are two values of c , say $c_* \in (0, c_1)$ and $c^* \in (c_1, c_0^*)$ such that (2.1) has a homoclinic orbit.

Figure 2 below includes a graph of the orbit of a solution satisfying (i) and (ii) projected onto the (u, q) plane, with the points t_1 and t_3 marked (as well as an additional point t_2 which is explained later). The other solution shown in that figure satisfies (i) but not (ii).

Theorem 1 is implied by Theorem 2 and the following result.

Theorem 3. If Conditions 1- 5 are satisfied then there is a c_1 satisfying the conditions in the second sentence of Theorem 2. Further, with this c_1 , if ε is sufficiently small, then the solution p_{ε,c_1} of (2.1) with $c = c_1$ satisfies (i) and (ii) of Theorem 2.

It will follow from the proofs of these results that as $\varepsilon \rightarrow 0$, $c^* \rightarrow c_0^*$. The following result is all we have proved about the asymptotic behavior of c_* .

Theorem 4.

$$\lim_{\varepsilon \rightarrow 0} c_* = 0.$$

However there is an $M > 0$ independent of ε such that if there is a homoclinic orbit for $c = c_*$ then $\frac{\varepsilon}{c_*} < M$.

Remark 2. For a given pair (ε, c_1) , the hypotheses of Theorem 2 can be verified by checking one solution of (2.2) at $c = c_1$ and one solution of (2.1), with the given ε and $c = c_1$. For the specific model considered in [4], standard numerical analysis (non-rigorous) easily finds specific values of (ε, c_1) where these hypotheses are apparently satisfied⁴. In the discussion section we describe how this could, in principle, be checked rigorously using uniform asymptotic analysis near the equilibrium points of (2.2) and (2.1), and then a rigorous numerical ode solver (using interval arithmetic) over two compact intervals. We cite a paper⁵ where a similar procedure was followed successfully, but we have not attempted it here.

Remark 3. In [4] only one homoclinic solution is found, and there is an extra hypothesis about the system (2.2). (Hypotheses 3.1) As far as we know, this hypothesis can only be checked by numerically solving the system (2.2).⁶ We discuss this further in Section 4.

3. PROOF OF THEOREM 2

3.1. The fast pulse. We need two simple preliminary results about the behavior of solutions.

Proposition 1. For any $\varepsilon \geq 0$ the regions $\left\{v < 0, w < 0, \frac{1}{1+\beta} < q < 1\right\}$ and $\left\{v > 1, w > 0, \frac{1}{1+\beta} < q < 1\right\}$ are positively invariant open sets for the system (2.1).

Proof. We are assuming that $0 < S(u) < 1$ for all u . Hence, $q' > 0$ if $q \leq \frac{1}{1+\beta}$ and $q' < 0$ if $q \geq 1$. Therefore $\left\{\frac{1}{1+\beta} < q < 1\right\}$ is positively invariant. Further, if $\frac{1}{1+\beta} < q < 1$ then $v'' = w' < 0$ if $v \leq 0$ and $w' > 0$ if $v \geq 1$. The result follows. \square

Note as well that because S is bounded, all solutions of (2.1) exist on $R = (-\infty, \infty)$.

Proposition 2. If $p = (u, v, w, q)$ is a solution of (2.1), and $u(t) \geq u_{knee}$ for some t , then either $q'(t) < 0$ or $q(t) < h(u_{knee})$.

Proof. This follows from Condition 3, which implies that the graph of the decreasing function $q = \frac{1}{1+\beta S(u)}$ in the (q, u) plane, where $q' = 0$, passes under the point $(u_{knee}, h(u_{knee}))$. (See Figure 1.) \square

In the first, and longest, part of the proof of Theorem 2 we show that there is a “fast” pulse, with speed $c^*(\varepsilon)$ which tends to c_0^* as ε tends to zero. In the second part we look for a “slow” pulse, with a speed $c_*(\varepsilon)$ which tends to zero as ε tends to zero.

We will show that for any possible homoclinic orbit, $u > 0$. We look for homoclinic orbits such that, as well, $q < q_0$ in $(-\infty, \infty)$. In searching for the fast solution we will consider for each $c > 0$ a certain uniquely defined solution

⁴For the parameter values used by Faye, a standard ode solver suggests that $(\varepsilon, c_1) = (.005, .34)$

satisfies the conditions in Theorem 2. If the conjecture in Remark 1 is true then it appears that $(\varepsilon, c_1) = (.05, .2)$ would work.

⁵(on the Lorenze equations)

⁶It appears to us that because of the degeneracy at the knee, it would be harder to verify this hypothesis rigorously than to do the same for (i) and (ii).

$p_c = (u_c, v_c, w_c, q_c)$ such that $p_c(-\infty) = p_0$. We will show that there is a nonempty bounded set of positive values of c , called $\Lambda(\varepsilon)$, such that, among other properties of p_c , either q_c exceeds q_0 at some point, or u_c becomes negative. We then examine the behavior of $p_{c^*(\varepsilon)}$ where $c^*(\varepsilon) = \sup \Lambda(\varepsilon)$. The goal is to show that $p_{c^*(\varepsilon)}(\infty) = p_0$. This is done by eliminating all the other possible behaviors of $p_{c^*(\varepsilon)}$, often by showing that a particular behavior implies that all values of c close to $c^*(\varepsilon)$ are not in $\Lambda(\varepsilon)$.

The following result is basic to our analysis of the full system (2.1). The proof is routine and again left to the appendix.

Lemma 3. *Suppose that Conditions 1- 5 hold, and let $p_0 = (u_0, u_0, 0, q_0)$ be the unique equilibrium point of (2.1). Then for any $\varepsilon \geq 0$ and $c > 0$ the system (2.1) has a one dimensional unstable manifold at p_0 , say $\mathcal{U}_{\varepsilon, c}$, with branch $\mathcal{U}_{\varepsilon, c}^+$ starting in the region $\{u > u_0, v > u_0, w > 0, \}$. If $p_{\varepsilon, c} = (u_{\varepsilon, c}, v_{\varepsilon, c}, w_{\varepsilon, c}, q_{\varepsilon, c})$ is a solution lying on this manifold, then for large negative t , $u_0 < u_{\varepsilon, c}(t) < v_{\varepsilon, c}(t)$ and $w_{\varepsilon, c}(t) > 0$. Also, $q_{0, c} \equiv q_0$, while if $\varepsilon > 0$ then $q_{\varepsilon, c}(t) < q_0$ for large negative t . The invariant manifold $\mathcal{U}_{\varepsilon, c}^+$ depends continuously on (ε, c) in $\varepsilon \geq 0, c > 0$. (The meaning of continuity here is made clear in the text below.) Finally, if $\lambda_1(c, \varepsilon)$ is the positive eigenvalue of the linearization of (2.1) around p_0 , then $\lambda_1(c, \varepsilon) > \lambda_1(c, 0)$ for each $c > 0$ and $\varepsilon > 0$.*

The following proposition follows trivially from (2.1) and will be used a number of times, often without specific mention.

Proposition 3.

$$\text{If } u' = 0 \text{ then } u'' = \frac{v'}{c}.$$

$$\text{If } u' = u'' = 0 \text{ then } u''' = \frac{v''}{c}.$$

$$\text{If } u' = u'' = u''' = 0 \text{ then } u^{iv} = -\frac{b^2}{c} q' S(u).$$

$$\text{If } q' = 0 \text{ then } q'' = -\frac{\varepsilon}{c} \beta q S'(u) u'$$

$$\text{If } w' = 0 \text{ then } v''' = w'' = b^2 (v' - q' S(u) - q S'(u) u').$$

$$\text{If } q' = u' = 0 \text{ then } q'' = 0 \text{ and } q''' = -\frac{\varepsilon}{c} \beta q S'(u) u'' = -\frac{\varepsilon}{c^2} \beta q S'(u) v'.$$

$$\text{If } q' = u' = v' = 0 \text{ then } q^{iv} = -\frac{\varepsilon}{c^2} \beta q S'(u) w' = -\frac{\varepsilon}{c^2} \beta q S'(u) v'' = -\frac{\varepsilon}{c} \beta q S'(u) u'''.$$

We use the fourth item in this list to prove

Lemma 4. *For any $\varepsilon > 0$ and $c > 0$, if p is a solution on $\mathcal{U}_{\varepsilon, c}^+$ and $u' \geq 0$ on an interval $(-\infty, \tau]$, then $q' < 0$ on $(-\infty, \tau)$.*

Proof. If u' never changes sign, let σ denote ∞ . Otherwise, suppose that u' first changes sign at σ . If $q'(\tau) = 0$ for some $\tau < \sigma$ and τ is the first zero of q' , then $q''(\tau) \geq 0$, and by the fourth item of Proposition 3, $u'(\tau) \leq 0$. From the definitions of σ and τ , $u'(\tau) = 0$ and so $q''(\tau) = 0$. Since u' does not change sign at τ , $u''(\tau) = 0$ and so $q'''(\tau) = 0$. Hence at τ ,

$$u' = u'' = q' = q'' = q''' = 0.$$

If $u'''(\tau) = 0$ then $p(\tau)$ is an equilibrium point, a contradiction. If $u'''(\tau) < 0$ then τ is a local maximum of u' , which is inconsistent with the assumption that $u' \geq 0$ on $(-\infty, \sigma]$. Hence $u_c'''(\tau) > 0$. But then $q^{iv}(\tau) < 0$. This again implies that $q' > 0$ on some interval to the left of τ , contradicting the definition of τ . This completes the proof of Lemma 4. \square

Lemma 5. *If $p = (u, v, w, q)$ is a solution on $\mathcal{U}_{\varepsilon, c}^+$ then $w > 0$ on an interval $(-\infty, \tau]$ with $u(\tau) = u_m$.*

Proof. Observe that $h(u) > q_0$ for $u_0 < u < u_m$. It follows that if $u_0 < u < u_m$ and $q < q_0$ on an interval $(-\infty, t)$, then $w' > 0$ on this interval. Hence $w > 0$ as long as $u_0 < u \leq u_m$ and $q < q_0$. (That is, if $u_0 < u \leq u_m$ and $q < q_0$ on $(-\infty, t]$, then $w > 0$ on this interval.) Since $u' > 0$ as long as $w = v' \geq 0$, Lemma 4 implies that $w > 0$ as long as $u_0 < u \leq u_m$, proving Lemma 5. \square

Hence the conditions $u(0) = u_m$ and $w > 0$ on $(-\infty, 0]$ determine a unique solution

$$p_{\varepsilon, c} = (u_{\varepsilon, c}, v_{\varepsilon, c}, w_{\varepsilon, c}, q_{\varepsilon, c})$$

on $\mathcal{U}_{\varepsilon, c}^+$.

Let

$$\Omega = \left\{ (u, v, w, q) \mid 0 < u < 1, 0 < v < 1, \frac{1}{1+\beta} < q < 1 \right\}.$$

Since $(u_0, u_0, 0, q_0) \in \Omega$, it follows from Proposition 1 that if $\mathcal{U}_{\varepsilon, c}^+$ is a homoclinic orbit, then it lies entirely in Ω .

In the rest of this subsection let c_1 and ε be chosen as in Theorem 2.

Lemma 6. *If $c \geq c_1$, then either $w_{\varepsilon, c} > 0$ on R , or at the first zero of $w_{\varepsilon, c}$, $u_{\varepsilon, c} > u_{knee}$.*

Proof. By the hypotheses on c_1 in Theorem 2, Lemma 2 implies that

$$u_{0, c}(T(c)) > u_{knee}.$$

To extend this to $\varepsilon > 0$ a comparison result is needed. Let $p = (u, v, w, q) = p_{\varepsilon, c}$. Lemma 4 implies that if $\varepsilon > 0$ then $q < q_0$ on any interval $(-\infty, t]$ where $w > 0$, since in such an interval $v' > 0$ and $u' > 0$. Also, as long as $w > 0$ we can consider u, w , and q as functions of v . Say that $u = U(v)$, $w = W(v)$, and $q = Q(v)$. Then

$$(3.1) \quad \begin{aligned} U'(v) &= \frac{v - U(v)}{cW(v)} \\ W'(v) &= \frac{b^2(v - Q(v)S(U(v)))}{W(v)} \end{aligned}$$

We compare $w = W(v)$ with the solution when $\varepsilon = 0$. Let $p_1 = p_{0, c}$. Then we can write $u_1 = U_1(v_1)$, $w_1 = W_1(v_1)$, and $q = q_0$. The equations become

$$(3.2) \quad \begin{aligned} U_1'(v) &= \frac{v - U_1(v)}{cW_1(v)} \\ W_1'(v) &= \frac{b^2(v - q_0 S(U_1(v)))}{W_1(v)} \end{aligned}$$

Since $\lambda_1(c, \varepsilon) > \lambda_1(c, 0)$ (Lemma 3), it is seen by considering eigenvectors of the linearization of (2.1) around p_0 ⁷ that for v sufficiently close to u_0 (i.e. for large

⁷The relevant matrix B is given in Appendix B.

negative t),

$$(3.3) \quad \begin{cases} U(v) < U_1(v) \\ W(v) > W_1(v) \end{cases}.$$

If, at some first \hat{v} , one of these inequalities should fail while the other still holds, then a contradiction results from comparing (3.1) and (3.2), because $q < q_0$ and S is increasing. For example, if $U(\hat{v}) = U_1(\hat{v})$ and $W(\hat{v}) > W_1(\hat{v}) > 0$, then (3.1) and (3.2) imply that $U'(\hat{v}) < U_1'(\hat{v})$, a contradiction because $U < U_1$ on (u_0, \hat{v}) . Also, if $W(\hat{v}) = W_1(\hat{v}) \geq 0$ and $U(\hat{v}) < U_1(\hat{v})$ then $W'(\hat{v}) > W_1'(\hat{v})$, since $q < q_0$ as long as $w \geq 0$. This is also a contradiction of the definition of \hat{v} .

If both inequalities fail at the same \hat{v} , then there is still a contradiction because $q < q_0$. Hence, if $W_1(v) \geq 0$ for $u_0 \leq v \leq \hat{v}$ then (3.3) holds in this interval.

This implies that for any $c \in (c_1, c_0^*)$, if $w_{\varepsilon, c}$ has a first zero at $T(\varepsilon, c)$, then $v_{\varepsilon, c}(T(\varepsilon, c)) > v_{0, c}(T(0, c))$. In the proof of Lemma 2 it is shown that $v_{0, c}(T(0, c)) > v_{0, c_1}(T(0, c_1))$, and combining these shows that if $u_{\varepsilon, c}(T(\varepsilon, c)) \leq u_{knee}$ and $v_{0, c_1}(T(0, c_1)) > q_0 S(u_{knee})$ then $w'_{\varepsilon, c}(T(\varepsilon, c)) > 0$. This contradiction completes the proof of Lemma 6. \square

Lemma 7. *If $c > c_0^*$, then $v_{\varepsilon, c} > 0$, $w_{\varepsilon, c} > 0$, $u'_{\varepsilon, c} > 0$, and $u_{\varepsilon, c} \rightarrow \infty$ as $t \rightarrow \infty$.*

Proof. This follows from Lemma 2 and the comparison used to prove Lemma 6. \square

We are now ready to apply a “shooting” argument to obtain the fast pulse. Still with ε as in Theorem 2, for each $c > 0$ let $p = p_{\varepsilon, c}$ and set

$\Lambda = \{c \geq c_1 \mid \text{There exist } t_1, t_2, \text{ and } t_3 \text{ such that } 0 < t_1 < t_2 < t_3 \text{ and}$

if $p = p_{\varepsilon, c}$ then $u' > 0$ on $[0, t_1)$, $u'(t_1) = 0$, $u(t_2) = u_0$, and either $u(t_3) = 0$ or $q(t_3) = q_0$.

Further, $u''(t_1) < 0$, $u' < 0$ on $(t_1, t_2]$ and $u < u_0$ on $(t_2, t_3]$.

(See Figures 2.)

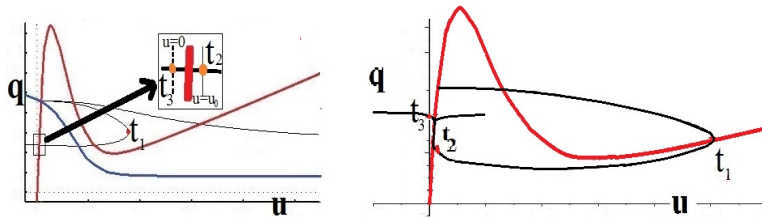


FIGURE 2. Each figure shows one solution with $c \in \Lambda$ and one solution with $c \notin \Lambda$.

Lemma 8. Λ is an open subset of the half line $c \geq c_1$.

Proof. Suppose that $c \in \Lambda$, and choose $t_3 = t_3(c)$ as in the definition of Λ . Note from (2.1) that if $u_c(t_3) = 0$ then there is a $\tau < t_3$ such that $v(\tau) = 0$, $v'(\tau) \leq 0$. Also, $v'' < 0$ if $v \leq 0$. Hence $v(t_3) < 0$ and $u'(t_3) < 0$.

Also, (2.1) implies that if $q(t_3) = q_0$ and $u(t_3) < u_0$ then $q'(t_3) > 0$. Since $p_c(t)$ is a smooth function of c , uniformly for t in, say, $(-\infty, t_3(c^*) + 1]$, it follows that for c in some neighborhood of c^* , $t_i(c)$ is defined for $i = 1, \dots, 3$ and all the inequalities in the definition of Λ continue to hold, so that this neighborhood lies in Λ . This proves Lemma 8. \square

The hypotheses of Theorem 2 imply that $c_1 \in \Lambda$, while by Lemma 7, if $c > c_0^*$, then $c \notin \Lambda$. The numbers t_i depend on c , and when we need to emphasize this we will denote them by $t_i(c)$, for $i = 1, 2, 3$.

We now let $c^* = \sup \Lambda$. (This is finite, by Lemma 7.)

Lemma 9. *With ε as in Theorem 2, $\mathcal{U}_{\varepsilon, c^*}^+$ is a homoclinic orbit of (2.1).*

Proof. The proof depends on the fact that c^* is a boundary point of Λ and lies in (c_1, c_0^*) . In Figure 4 we show several graphs of (u, q) which, if they occurred for $p_{\varepsilon, c}$, would suggest (without quite implying) that c was on the boundary of Λ . We must eliminate these and some other possibilities, and this will imply that $p_{\varepsilon, c^*}(\infty) = (u_0, u_0, 0, q_0)$. The reader may want to review the definition of Λ before examining these figures.

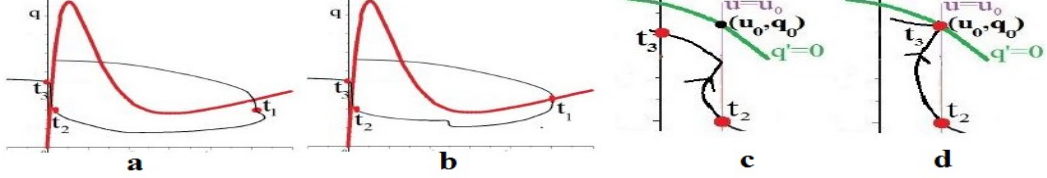


FIGURE 3. Several possibilities if c is on the boundary of Λ

We need additional lemmas. Recalling that ε was chosen in the statement of 2, we will now drop the ε -dependence of $p_{\varepsilon, c}$ and its components from our notation, writing p_c and Λ . When the dependence of p_c on c is not crucial to an argument we will use u, v, w, q for its components.

Lemma 10. *Suppose that $p = (u, v, w, q)$ is a non-constant solution of (2.1) satisfying one of the following sets of conditions at some τ :*

- (i) $u'(\tau) = 0$, $v'(\tau) = 0$, $w'(\tau) \leq 0$, $q'(\tau) \leq 0$, $u(\tau) \geq u_0$
- (ii) $u'(\tau) = 0$, $v'(\tau) < 0$, $w'(\tau) = 0$, $q'(\tau) = 0$, $u(\tau) \geq u_0$
- (iii) $u'(\tau) = 0$, $v'(\tau) \leq 0$, $q'(\tau) > 0$, $u(\tau) = u_0$.
- (iv) $u'(\tau) = 0$, $v'(\tau) \leq 0$, $w'(\tau) > 0$, $q'(\tau) \geq 0$, $u(\tau) \geq u_0$

Then $p(\tau) \notin \mathcal{U}_{\varepsilon, c^}^+$.*

Proof. Suppose that (i) holds. Then $w'(\tau)$ and $q'(\tau)$ cannot both vanish. If $w'(\tau) = 0$ and $q'(\tau) < 0$ then $w''(\tau) = -b^2 q'(\tau) S(u(\tau)) > 0$. Hence in some interval $(\tau - \delta, \tau)$,

$$(3.4) \quad w' < 0 \text{ and } q' < 0.$$

If $q'(\tau) = 0$ and $w'(\tau) < 0$ then

$$\begin{aligned} q''(\tau) &= -\frac{\varepsilon}{c} \beta q(\tau) S'(u(\tau)) u'(\tau) = 0 \\ q'''(\tau) &= -\frac{\varepsilon}{c^2} \beta q(\tau) S'(u(\tau)) v'(\tau) = 0 \\ q^{(iv)}(\tau) &= -\frac{\varepsilon}{c^2} \beta q(\tau) S'(u(\tau)) w'(\tau) > 0. \end{aligned}$$

Once again we see that (3.4) holds on some interval $(\tau - \delta, \tau)$.

Consider the “backward” system satisfied by $P(s) = p(\tau - s)$. If $P = (U, V, W, Q)$ then

$$(3.5) \quad \begin{aligned} U' &= \frac{U-V}{c} \\ V' &= -W \\ W' &= b^2 (QS(U) - V) \\ Q' &= \frac{\varepsilon}{c} (Q + \beta QS(U) - 1) \end{aligned}.$$

Also,

$$(3.6) \quad U'(0) = 0, V'(0) = 0, W'(0) \geq 0, \text{ and } Q'(0) \geq 0.$$

From (3.4) and (3.6) it follows that on some interval $0 < s < \delta$,

$$(3.7) \quad U' > 0, V' < 0, W' > 0 \text{ and } Q' > 0.$$

We claim that these inequalities hold for all $s > 0$. If, on the contrary, one of them fails at a first $s_0 > 0$, then

$$(3.8) \quad U(s_0) > U(0), V(s_0) < V(0), W(s_0) > W(0), \text{ and } Q(s_0) > Q(0).$$

But (3.8), (3.5), and (3.6) imply that at s_0 , all of the inequalities in (3.7) still hold, because $S' > 0$. This contradiction implies that U , W , and Q continue to increase, and V continues decrease on $0 < s < \infty$, and in particular, U does not tend to u_0 as $s \rightarrow \infty$. Thus, $p(\tau) \notin \mathcal{U}_{\varepsilon, c^*}^+$.

The proofs in cases (ii), (iii) and (iv) are similar and left to the reader. This completes the proof of Lemma 10. \square

We now begin our study of the properties of p_{c^*} . Lemma 10 will assist us in proving the following result.

Lemma 11. *The number $t_1(c^*)$ is still defined, as the first zero of u'_{c^*} , and $u''_{c^*}(t_1(c^*)) < 0$. Either $\mathcal{U}_{\varepsilon, c^*}^+$ is homoclinic or $t_2(c^*)$ is still defined, as the first zero of $u - u_0$. Also, if $\mathcal{U}_{\varepsilon, c^*}^+$ is not homoclinic then $u'_{c^*} < 0$ on $(t_1, t_2]$.*

Remark 4. *This lemma eliminates the graph in Figure 3.1-a.*

Proof. Suppose that $t_1(c^*)$ is not defined. Then $u'_{c^*} > 0$ on $(-\infty, \infty)$. Since p_0 is the only equilibrium point of (2.1), this implies that for some τ , $v_{c^*}(\tau) > u_{c^*}(\tau) > 1$ and $v'_{c^*}(\tau) > 0$. Then these inequalities hold at τ for nearby c , and by Proposition 1, $v_c(t) > 1$ for $t > \tau$. Hence $u_c > 1$ on $[\tau, \infty)$ and so $c \notin \Lambda$, contradicting the definition of c^* . Therefore $t_1(c^*)$ is defined.

We now show that $u''_{c^*}(t_1) < 0$. Again assume that $p = p_{c^*}$, and suppose that $u''(t_1) = 0$. If $u'''(t_1) < 0$ then t_1 is a local maximum of u' , which is not possible because t_1 is the first zero of u' . Hence at t_1 , $u''' = \frac{b^2}{c^*}(v - qS(u)) \geq 0$. If $u'''(t_1) = 0$, then at t_1 ,

$$u^{(iv)} = \frac{w''}{c} = -\frac{b^2}{c}q'S(u) > 0,$$

by Lemma 4. This implies that u' changes sign from negative to positive at t_1 , again a contradiction of the definition of t_1 . Hence at t_1 ,

$$u''' = \frac{b^2}{c^*}(v - qS(u)) > 0,$$

or $q(t_1) < \frac{v(t_1)}{S(u(t_1))} = \frac{u(t_1)}{S(u(t_1))}$, since $u'(t_1) = 0$. Also, $u'' > 0$ in some interval $(t_1, t_1 + \delta)$. However u is bounded by 1 and does not tend to a limit above u_0 . Therefore u' changes sign at some $\tau > t_1$ (c^*). Since $u' \geq 0$ on $(-\infty, \tau]$, $v \geq u$ on this interval. At τ , $u'' \leq 0$, and so there is a point σ in (t_1, τ) such that $u'' = 0$ and $u''' = \frac{v'' - u''}{c} = \frac{w'}{c} \leq 0$. Hence at σ , $q \geq \frac{v}{S(u)} \geq \frac{u}{S(u)}$. But by Lemma 17 $u(t_1) \geq u_{knee}$, and $h(u) = \frac{u}{S(u)}$ is increasing in (u_{knee}, ∞) , so $q(\sigma) > q(t_1)$, again a contradiction of Lemma 4. We have therefore proved the first sentence of Lemma 11.

Lemma 12. *If $p = p_{c^*}$, then $u' < 0$ as long after t_1 as $q' \leq 0$.*

Proof. Suppose instead that there is a first $\tau > t_1$ such that $q' \leq 0$ on $(-\infty, \tau]$ but $u'(\tau) = 0$. Then $u''(\tau) \geq 0$. First consider the case $q' < 0$ on $(-\infty, \tau]$.

If $u''(\tau) > 0$ then u'_{c^*} changes from negative to positive before $q' = 0$, and this will be true as well for c close to c^* , contradicting the definition of c^* . Hence suppose that $u''(\tau) = \frac{v'(\tau)}{c^*} = 0$. If $u''' > 0$, then u' has a local minimum at τ , contradicting the definition of τ . Hence

$$u'''(\tau) = \frac{w'(\tau)}{c^*} \leq 0.$$

But now the conditions in (i) of Lemma 10 are satisfied, giving a contradiction.

We have left to consider the case that $q'(\tau) = u'(\tau) = 0$. Then $q''(\tau) = 0$. If $u''(\tau) > 0$ then $q'''(\tau) < 0$ so $q' < 0$ in an interval $(\tau, \tau + \delta)$. Hence in this case, u' changes sign (from negative to positive) before $q' > 0$. For c close to c^* there are two possibilities: either u'_c changes sign from negative to positive before $q'_c > 0$, and so before $u = u_0$, or else $u'_c < 0$ in a neighborhood of τ , but in a neighborhood of, say, $\tau + \frac{1}{2}\delta$, $u'_c > 0$ and $u > u_0$. (See Figure 4) Neither of these possibilities occurs if $c \in \Lambda$, so once again, $c^* \notin \partial\Lambda$, a contradiction. This proves Lemma 12. \square

It follows that there is a first $\tau_1 > t_1$ such that $q'_{c^*}(\tau_1) = 0$. Also, $u'_{c^*}(\tau_1) < 0$, and (equivalently by the fourth item of Proposition 3) $q''_{c^*}(\tau_1) > 0$.

Lemma 13. *$q'_{c^*} > 0$ and $u'_{c^*} < 0$ as long after τ_1 as $u_{c^*} \geq u_0$.*

Proof. This lemma eliminates the graph in Figure 3.1-b.

Let $p = p_{c^*}$. Since $q''(\tau_1) > 0$, $q' > 0$ and $u' < 0$ on some interval $(\tau_1, \tau_1 + \delta]$ with $\delta > 0$. We claim that $q' > 0$ on any such half-closed interval in which $u' < 0$. This follows because, by Proposition 3, $q'' > 0$ at any point where $q' = 0$ and $u' < 0$.

We next show that $u' < 0$ on any interval $(\tau_1, \tau_1 + \delta]$ in which $q' > 0$ and $u \geq u_0$. If not, then there is a first $\sigma > \tau_1$ with $u'(\sigma) = 0$, $q'(\sigma) > 0$ and $u \geq u_0$ on $(-\infty, \sigma]$. Then $u''(\sigma) \geq 0$. If $u''(\sigma) > 0$, then $u'_{c^*} > 0$ in some interval $(\sigma, \sigma + \delta)$. In this

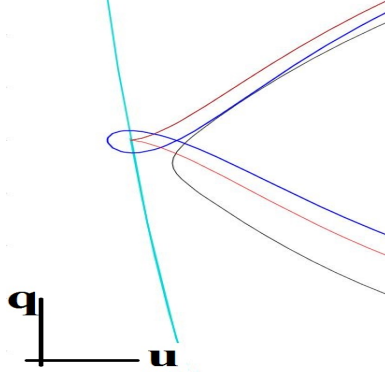


FIGURE 4. (u_c, q_c) for $c = c^*$ (with cusp), and two other solutions with $c \notin \Lambda$. The graph of a decreasing function is part of the q nullcline.

case, for c close enough to c^* , u'_c changes sign after t_1 but before $u_c < u_0$ or else u_c crosses u_0 and back again, and such c cannot lie in Λ , a contradiction.

Hence, $u''(\sigma) = 0$. But then, because $u(\sigma) = v(\sigma)$,

$$u'''(\sigma) = \frac{b^2}{c^*} (v - qS(u)) = \frac{b^2}{c^*} (u - qS(u)).$$

In the region where $q' > 0$ and $u \geq u_0$, $q < \frac{u}{s(u)}$. Hence, $u'''(\sigma) > 0$ and again $u'_{c^*} > 0$ in an interval to the right of σ but before $u_{c^*} < u_0$, a contradiction as before.

The only other possibility contradicting Lemma 13 is that there is a first $\tau > \tau_1(c^*)$ where $u_{c^*}(\tau) \geq u_0$ and $q'_{c^*}(\tau) = u'_{c^*}(\tau) = 0$. We consider two cases: (a) $q_{c^*}(\tau) < q_0$ and $u_{c^*}(\tau) > u_0$, and (b) $q_{c^*}(\tau) = q_0$, $u_{c^*}(\tau) = u_0$. First consider (a). In an interval $(\tau - \delta, \tau)$, $q'_{c^*} > 0$, $u'_{c^*} < 0$, and $u_{c^*} > u_0$, and so at τ , if $p = p_{c^*}$, then

$$u' = 0, \quad u'' \geq 0, \quad q' = 0, \quad q'' = 0.$$

Also,

$$q''' = -\frac{\varepsilon}{c} \beta q S'(u) u'' \leq 0.$$

But $u'_{c^*}(\tau) > 0$ is impossible because it means that even for nearby c , $u'_c > 0$ after t_1 but before $u = u_0$. Therefore at τ , $q''' = 0$ and $u'' = 0$. Then

$$q^{(iv)} = -\frac{\varepsilon}{c} q S''(u) u''.$$

But on the nullcline $q' = 0$, with $u > u_0$, $u' = 0$, and $u'' = 0$,

$$(3.9) \quad u''' = \frac{v''}{c^*} = \frac{b^2}{c^*} (v - qS(u)) = \frac{b^2}{c^*} (u - qS(u)) > 0.$$

This implies that u' has a local minimum at τ , whereas we know that $u' < 0$ in (t_1, τ) . This contradicts the definition of τ .

Turning to case (b), we now have that at τ ,

$$u' = 0, \quad q' = 0, \quad q'' = 0, \quad (u, q) = (u_0, q_0).$$

Thus $w'(\tau) = 0$. If $u''(\tau) > 0$ then $u' > 0$ to the right of τ . As before, if c is close to c^* then either u_c crosses u_0 twice, or p_c doesn't reach the region $u < u_0$ before $u' > 0$, both of which mean that $c \notin \Lambda$.

If $u''(\tau) = \frac{w(\tau)}{c} = 0$ then $p(\tau)$ is again an equilibrium point. The third possibility, $u''(\tau) = \frac{v'(\tau)}{c^*} < 0$ implies that (ii) of Lemma 10 is satisfied, and thus again gives a contradiction. This completes the proof of Lemma 13. \square

If $u > u_0$ on R then $u'_{c^*} < 0$ and $q' > 0$ on (τ_1, ∞) , and $\mathcal{U}_{\varepsilon, c^*}^+$ is homoclinic. This proves Lemma 11. \square

Thus, for $p = p_{c^*}$ if $\mathcal{U}_{\varepsilon, c^*}^+$ is not homoclinic then t_2 exists with $u(t_2) = u_0$ and $u' < 0$ on $(t_1, t_2]$. However, there is no t_3 such that $u < u_0$ on $(t_2, t_3]$ and either $u(t_3) = 0$ or $q(t_3) = q_0$, for otherwise $c^* \in \Lambda$, and this has already been ruled out.

Therefore if $t > t_2(c^*)$ then $0 < u_{c^*} \leq u_0$ and $q_{c^*} \leq q_0$, for otherwise nearby values of c are once again not in Λ . If $\mathcal{U}_{\varepsilon, c^*}^+$ is not homoclinic and $p = p_{c^*}$, then there must be a first $\tau > t_2(c^*)$ with $u(\tau) = u_0$, $u'(\tau) = 0$, $q(\tau) \leq q_0$ and $u''(\tau) \leq 0$.

Suppose that this is the case and also $q(\tau) < q_0$. (This is pictured in Figure 3.1-c.)

Then $q'(\tau) > 0$. If $u''(\tau) \leq 0$, then (iii) of Lemma (10) applies and gives a contradiction. Hence $q(\tau) = q_0$. Then at τ , $q' = u' = w' = 0$ and $u'' = \frac{v'}{c^*} < 0$. (This is pictured in Figure 3.1-d. But this is case (ii) of Lemma 10 and so also impossible.

We have established that if $\mathcal{U}_{\varepsilon, c^*}^+$ is not homoclinic (with $u > u_0$ on R) then for large t , $0 < u_{c^*}(t) < u_0$ and $q'_{c^*} > 0$. This is only possible if $\mathcal{U}_{\varepsilon, c^*}^+$ is homoclinic (with $q_{c^*} < q_0$ and $u'_{c^*} > 0$ for large t). This proves Lemma 9. \square

To complete the proof of Theorem 2 we look for a second homoclinic orbit, with $c < c_1$.

3.2. The slow pulse. Again we adapt the method in [10]. It is stated so as to be useful in the proofs of Theorems 3 and 4, as well as Theorem 2.

Lemma 14. *There are $\hat{c} > 0$ and $M > 0$, both independent of ε , such that if $0 < c < \hat{c}$ and $\frac{\varepsilon}{c} > M$ then the solution p_c remains in the region $v > u$ on $(-\infty, \infty)$, and u crosses $u = 1$.*

Proof. Since the proof uses some of the easier parts of the proof of Lemma 2, it is included in the appendix. \square

From here to the end of this section the parameters ε and c_1 remain as in the previous subsection. Lemma 14 implies that if we extend Λ to $(0, c_0^*)$, with otherwise the same definition as above, then $\inf \Lambda > 0$. This suggests that $\inf \Lambda$ corresponds to a homoclinic orbit. The problem with this argument is that the concept of “front” in the sense used in the method of geometric perturbation, breaks down for small c . The slow homoclinic orbit is not close, even up to the first zero of u'_c , to the front found when $\varepsilon = 0$. More precisely, our proof of the first sentence of Lemma 11 is no longer valid, because we cannot assert that the first zero of u'_c occurs with $u_c > u_{knee}$. Hence we must modify our “shooting set” on the c axis. This requires several steps.

Our argument from here no longer refers to a point t_1 where u'_c changes sign, but instead considers solutions such that q'_c changes sign. Let

$$\Sigma = \{c \in (0, c_1] \mid \text{There is a } \tau_1 > 0 \text{ such that } q'_c < 0 \text{ on } (-\infty, \tau_1), \\ q'_c(\tau_1) = 0, \text{ and } u'_c(\tau_1) < 0\}.$$

Our argument does not require that if $c \in \Sigma$ then u'_c has only one zero in $(-\infty, \tau_1)$, though numerically this appears to be the case.

$$\Sigma_1 = \{c \in \Sigma \mid q'_c > 0 \text{ on any interval } (\tau_1, T) \text{ in which } u_c > 0 \text{ and } q_c < q_0\}.$$

Recall that ε and c_1 were chosen so that u'_{c_1} has a unique zero. As in the proof of Lemma 13, this implies that q'_{c_1} has a unique zero, say τ_{c_1} , and $u'_{c_1}(\tau_{c_1}) < 0$. Hence $c_1 \in \Sigma_1$. Also, Lemma 14 shows that there is an interval $(0, c_2)$ which contains no points of Σ .

Let

$$c_3 = \sup \{c < c_1 \mid c \notin \Sigma\}.$$

Lemma 15. *There is a τ_1 such that $q'_{c_3} < 0$ on $(-\infty, \tau_1)$, $q'_{c_3}(\tau_1) = 0$, $q''_{c_3}(\tau_1) = 0$, and $q'''_{c_3}(\tau_1) < 0$.*

Proof. If $q'_c < 0$ on R then there is a $\sigma > 0$ such that $u_{c_3}(\sigma) = 1$ and $u'_{c_3}(\sigma) > 0$. From the continuity of $p_c(t)$ with respect to c , the same is true for u_c if c is sufficiently close to c_3 . In particular, again $q'_c < 0$ on $(-\infty, \infty)$. But then $c \notin \Sigma$, contradicting the definition of c_3 .

Therefore a first τ_1 is defined such that $q'_{c_3}(\tau_1) = 0$. Then $q''_{c_3}(\tau_1) \geq 0$. Also, by Proposition 3, $q''_{c_3}(\tau_1) = -\beta S'(u_{c_3}(\tau_1))u'_{c_3}(\tau_1)$. If $q''_{c_3}(\tau_1) > 0$ then by the implicit function theorem, $\tau_1(c)$ is defined for nearby c as the first zero of q'_c , with $q''_c(\tau_1(c)) > 0$ and $q'_c < 0$ on $(-\infty, \tau_1(c))$, contradicting the definition of c_3 . Hence $q''_{c_3}(\tau_1) = u'_{c_3}(\tau_1) = 0$. If $q'''_{c_3}(\tau_1) > 0$ then τ_1 is a local minimum of q'_{c_3} , contradicting the definition of τ_1 . If $q'''_{c_3}(\tau_1) = 0$ then $q^{iv}_{c_3}(\tau_1) = -\frac{\varepsilon}{c_3}\beta q_{c_3}(\tau_1)S'(u_{c_3}(\tau_1))w'_{c_3}(\tau_1)$, and since $q'_{c_3}(\tau_1) = 0$ and $q_{c_3}(\tau_1) < q_0$, $w'_{c_3}(\tau_1) > 0$ and $q^{iv}_{c_3}(\tau_1) < 0$. This implies that $q'_{c_3} > 0$ on an interval $(\tau_1 - \delta, \tau_1)$, again a contradiction. Hence $q'''_{c_3}(\tau_1) < 0$, completing the proof of Lemma 15. \square

Thus, $q'_{c_3} < 0$ in some interval $(\tau_1, \tau_1 + \delta)$. This result implies that $c_3 \notin \Sigma$. However the interval $(c_3, c_1] \subset \Sigma$. Lemma 15 also implies that points in $(c_3, c_1]$ near to c_3 are not in Σ_1 , since the corresponding solutions on $\mathcal{U}_{\varepsilon, c}^+$ must have a change of sign of q'_c from positive to negative after $\tau_1(c)$. Let

$$c_* = \inf \{c > c_3 \mid c \in \Sigma_1\}.$$

We claim that $\mathcal{U}_{c_*}^+$ is a homoclinic orbit.

The proof uses techniques very similar to those above. First observe that $c_* > c_3$ and $c_* \in \Sigma$. Therefore $\tau_1 = \tau_1(c_*)$ is defined as in the definition of Σ . Then use the following result.

Lemma 16. *If $c \in \Sigma_1$, then $u'_c < 0$ on any interval $[\tau_1(c), \tau_1(c) + \delta]$ in which $u_c \geq u_0$.*

Proof. If $u'_c = 0$ at some first $\sigma > \tau_1$ with $u_c(\sigma) \geq u_0$, then $u''_c(\sigma) \geq 0$. But in the region where $u \geq u_0$ and $q' > 0$, w' is positive, and this implies that p_c crosses into $q' < 0$, a contradiction of the definition of Σ_1 . \square

Corollary 1. *If $\mathcal{U}_{\varepsilon, c_*}^+$ is not homoclinic then there is a $t_2 > \tau_1$ such that $u_{c_*}(t_2) = u_0$ and $u'_{c_*} < 0$ on $[\tau_1, t_2]$. Further, $u_{c_*} < u_0$ on (t_2, ∞) .*

Proof. Let $p = p_{c_*}$. Lemma 16 implies the existence of t_2 . Suppose there is a first $\sigma > t_2$ with $u(\sigma) = u_0$. From the definitions of Σ_1 and c_* , $q' \geq 0$ on $[\sigma, \infty)$. Since $\frac{1}{1+\beta S(u)}$ is decreasing and $q' > 0$ if $q < \inf \frac{1}{1+\beta S}$, u cannot increase indefinitely. Hence there is a $\rho \geq \sigma$ with

$$\begin{aligned} u(\rho) &\geq u_0, u'(\rho) = 0, u''(\rho) = \frac{v'(\rho)}{c} = \frac{w(\rho)}{c} \leq 0 \\ w'(\rho) &> 0, q'(\rho) \geq 0. \end{aligned}$$

A contradiction then results from (iv) of Lemma 10. \square

Now apply the technique of Lemma 8, including use of Proposition 3 and Lemma 10, to show that $u_{c_*} > 0$ and $q_{c_*} < q_0$ on (t_2, ∞) . In particular, Lemma 10 is used to show that there is no $t > t_2$ (in fact, no t at all) with $(u_{c_*}(t), q_{c_*}(t)) = (u_0, q_0)$. It follows that on (t_2, ∞) , $q'_{c_*} > 0$, and so indeed, $\mathcal{U}_{\varepsilon, c_*}^+$ is homoclinic. This completes the proof of Theorem 2.

3.3. Proofs of Theorems 1, 3 and 4. As mentioned above, Theorem 1 follows from Theorems 2 and 3. In Theorem 3 ε is not fixed. Also, c_1 is any number in $(0, c_0^*)$, which however is fixed at this stage for the rest of this section.

Let $I = [c_1, c_0^* + 1]$. We note that the unstable manifold $\mathcal{U}_{\varepsilon, c}^+$ varies continuously with (ε, c) for $\varepsilon \geq 0$ and $c \in I$. To be more precise, if $p_{\bar{\varepsilon}, \bar{c}}$ exists on $(-\infty, T]$ then in some neighborhood of $(\bar{\varepsilon}, \bar{c})$, $p_{\varepsilon, c}(t)$ exists for $-\infty < t \leq T$ and is a continuous function of (ε, c, t) .⁸

From the third sentence of Lemma 2 it follows that c_1 can be chosen in $(0, c_0^*)$ such that if $c_1 \leq c < c_0^*$, then $v_{0, c}(T(c)) > q_0 S(u_{knee})$, where $T(c)$ is the unique zero of $w_{0, c}$. This proves the first assertion of Theorem 3. We now choose c_1 in this way.

Lemma 17. *There is an $\varepsilon_0 > 0$ and a $\tau > 0$ such that if $0 < \varepsilon < \varepsilon_0$ and $c \in I = [c_1, c_0^* + 1]$, then $u_{\varepsilon, c}(t) = u_{knee}$ for some first $t \leq \tau$, and $w_{\varepsilon, c} > 0$ on $(-\infty, \tau]$. (Hence, $p_{\varepsilon, c}$ satisfies the first condition of Theorem 2.) Further, ε_0 can be chosen so that p_{ε, c_1} satisfies conditions (i) and (ii) of Theorem 2.*

Proof. From the choice of c_1 , Lemma 2 implies that for any $c \geq c_1$, there is a $\delta > 0$ such that if $c \in I$ then $v'_{0, c} = w_{0, c} \geq \delta$ in the interval $[0, \tau]$ where $u_m \leq u \leq u_{knee}$. From $cu' = v - u$ it follows that for some $\tau > 0$, if $c_1 \leq c \leq c_0^*$ then $u_{0, c} = u_{knee}$ before $t = \tau$. The uniform continuity of $u_{0, c}(t)$ in (ε, c, t) , for $-\infty < t \leq \tau$ and $d \in I$ in any compact interval $[0, \hat{\varepsilon}]$ with $\hat{\varepsilon} > 0$, then implies the first conclusion of the Lemma. The remaining assertion of Lemma 17 follows by similar arguments. \square

We have now proved Theorems 2, 3, and 1, in that order. To prove Theorem 4 apply a continuity argument similar to that just used to show that for any $\delta > 0$ there is an ε_1 such that if $\delta \leq c \leq c_0^* - \delta$ and $0 < \varepsilon < \varepsilon_1$, the pair (ε, c) satisfy the hypotheses on (ε, c_1) in Theorem 2. It follows that pulses exist for some $c_* \in (0, \delta)$ and some $c^* \in (c_0^* - \delta, c_0^*)$. But Lemma 14 implies that $\frac{\varepsilon}{c_*} < M$. Theorem 4 follows.

⁸See the footnote at the end of the appendix for a further discussion of this point.

4. DISCUSSION

4.1. Hypothesis 3.1 of [4]. As stated earlier, there is an additional hypothesis in the existence result given in [4], namely Hypothesis 3.1 in that paper. This hypothesis is interesting in a broader context, and we will include some comments on its relation to the well-known pde model of FitzHugh and Nagumo.

To state this hypothesis we need to introduce a basic tool in the method of geometric perturbation, the so-called “singular” solution. The singular solution of (2.1) is a continuous piecewise smooth curve in R^4 consisting of four smooth pieces.

The first piece is the front with speed c_0^* found in Lemma 1. (Recall that “fronts” were defined just after the statement of this lemma.) In Figure 5 the green line segment is the projection of the graph of the front onto the (u, q) plane.

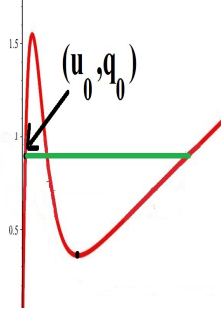


FIGURE 5. The red curve is the graph of $q = \frac{u}{S(u)}$

The second piece of the singular solution is a segment of the nullcline $u = qS(u)$ (with $w = 0$, $v = u$) as shown in Figure 6. It is obtained from (2.1) by letting $p(t) = P(\varepsilon t)$, formally setting $\varepsilon = 0$ in the resulting system of ode's for $P = (U, V, W, Q)$, and solving the resulting set of one differential equation and three algebraic equations, one of which is $U - QS(U) = 0$. For more information on this segment, and the singular solution in general, see [4]. We don't need to say more about this segment here.

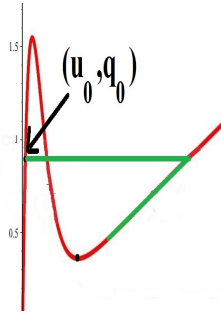


FIGURE 6. The first two segments of the singular solution

To define the third part of the singular solution (crucial in Hypothesis 3 of [4]), we consider the fast system (2.2), but with q_0 replaced by q , as a parameter ranging between q_{\min} and q_0 .

$$(4.1) \quad \begin{aligned} u' &= \frac{v-u}{c} \\ v' &= w \\ w' &= b^2 (v - qS(u)) \end{aligned}$$

For each $q \in (q_{\min}, q_0]$ there is a unique $c(q) \geq 0$ such that (4.1) has a bounded non-constant solution

$$r_{c(q)} = (u_{c(q)}, v_{c(q)}, w_{c(q)}) .$$

The graph of this solution is a heteroclinic orbit connecting the left and right branches of $q = \frac{u}{S(u)}$ in the (u, q) plane. There is at least one value of $q \in (q_{\min}, q_0)$ such that $c(q) = 0$. This will be true for any q such that

$$\int_{u_-(q)}^{u_+(q)} (qS(u) - u) du = 0.$$

For $q \in (q_{\min}, q_0)$ and sufficiently close to q_{\min} , the integral above is negative, and whenever this is the case, the connecting heteroclinic orbit exists for some $c(q) > 0$, but unlike the front defined earlier, $u_{c(q)}$ is decreasing, from $u_+(q)$ to $u_-(q)$. Such a solution is called a “back”. If $q = q_{\min}$ then there is a “back” for any $c \geq \lim_{q \rightarrow q_{\min}^+} c(q)$. All this can be proved using methods from the appendix, or see [4].

The third part of the singular solution of (2.1) is a “back”, at a value $q = q_1 \in [q_{\min}, q_0)$ with speed $c = c(q_0)$. There must be at least one q_1 for which such a back exists. As far as we know there is no proof that c is a monotone function of q in (q_{\min}, q_0) , so possibly there could be more than one such q_1 . In this case we can require that the jump down is at the largest possible q_1 supporting a back with speed $c(q_0)$. The singular solution is said to “jump down above the knee” if $q_1 > q_{\min}$.

Numerical computations suggest that often no such q_1 exists in (q_{\min}, q) . In this case, there is still a traveling back with speed $c(q_0)$, but it is at $q_1 = q_{\min}$.

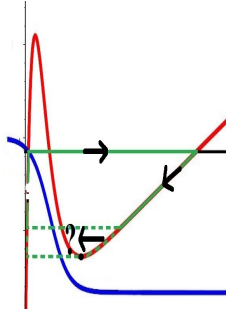


FIGURE 7. Nullclines: Red, Blue; Singular solution: Green

The fourth part of the singular solution is a slow return along the left branch of the nullcline.

Hypotheses of Faye:

- (i) The system (2.1) has a unique equilibrium point $(u_0, u_0, 0, q_0)$.
(ii) If $h(u) = \frac{u}{S(u)}$ then the equation

$$g(u) = q_0$$

has exactly three solutions, $u_0 < u_m < u_+$, with $h'(u_0) > 0$, $h'(u_m) < 0$, and $h'(u_+) > 0$.

(iii)

$$\int_{u_0}^{u_+} (q_0 S(u) - u) du > 0.$$

- (iv) The speed of any “back” with $q \in (q_{\min}, q_0)$ is less than $c(q_0)$.

It follows that the back of the singular solution is required to be at the knee. This condition can only be verified by numerical integration of the fast system.

Theorem 5. (Faye): Under hypotheses (i), (ii), (iii), and (iv), if ε is sufficiently small then the system (2.1) has a homoclinic orbit for at least one positive value of c .

Geometrical perturbation, based on work of Fenichel and others, is a technique for showing that the singular solution is close to a real solution if ε is sufficiently small. Certain “transversality” conditions can be complicated to check, requiring a technique called “blow-up”.

We can contrast the existence of a back at the knee with the well-known behavior of the pde model of FitzHugh and Nagumo. (See [10] for a presentation of this model and a proof that it has two traveling pulses.) The fast FitzHugh-Nagumo pulse can be described as having a jump up, (close to a front) during which u increases rapidly while w is nearly zero, followed by a slow increase in w , and then a jump down (close to a back), with w again nearly constant (but positive), and u decreasing rapidly. In this case, the back occurs before (u, w) reaches the knee. See 8.

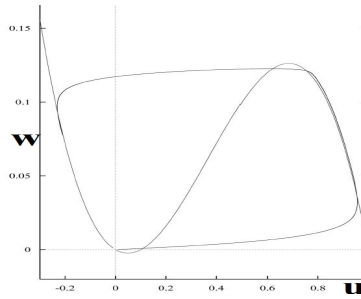


FIGURE 8. FitzHugh-Nagumo pulse (u, v) plane

We have done some preliminary numerical investigation to test whether it is possible, in the model studied in this paper and with the particular function S in (1.3), to adjust the parameters λ and κ so that the jump down occurs before w reaches the knee. We have not found such a pair (λ, κ) , but we cannot assert that none exists.

For the FitzHugh-Nagumo model, however, it is clear that the jump down is always before reaching the knee. This follows because the reaction term in equations is a cubic polynomial, $f(u) = u(1-u)(u-a)$, where $0 < a < \frac{1}{2}$. This function is symmetric around its inflection point, which leads to the "before the knee" behavior of the singular solution.

So we searched numerically for alternative functions to use for f which, while still "cubic like", permit the down jump of the singular solution to be at the knee. We found such a function, as illustrated in Figure 9. We are not aware of a method which determines analytically where the downjump occurs, either for the model of Faye or that of FitzHugh-Nagumo when f is asymmetric.

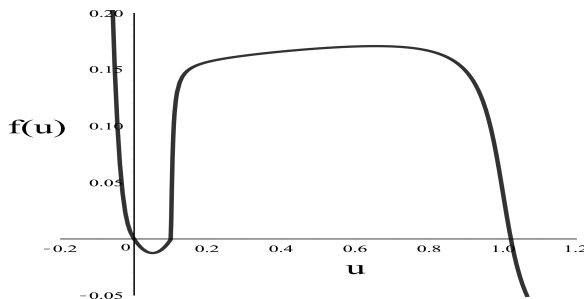


FIGURE 9. a "cubic-like" function for an alternative FitzHugh-Nagumo type model

The existence proof in [10] for fast and slow homoclinic orbits of the FitzHugh-Nagumo system also applies to functions f such as that pictured in Figure 9. On the other hand it appears that the proof by geometric perturbation in this case, while probably still basically valid, requires a more complicated analysis because the downjump of the singular solution may occur at the knee.

4.2. The slow pulse. It appears that the fast-slow analysis used to get the singular solution, for any of the models we have discussed, does not apply to the slow pulse. Hence it appears difficult to use geometric perturbation to obtain this solution. In [[15] this solution was obtained in the FitzHugh-Nagumo case using dynamical systems methods, but only for a sufficiently close to $\frac{1}{2}$.

The analysis in [15] was in the region a close to $\frac{1}{2}$, ε and c small. Indeed, if $a = \frac{1}{2}$ then there is only one pulse and it is a standing wave ($c = 0$). It is proved in [15] that for $\frac{1}{2} - a$ positive but small there is a smooth curve $(c, \varepsilon(c))$ corresponding to pulse solutions and connecting c_* to c^* . The speeds c_* and c^* , and the maximum of $\frac{\varepsilon(c)}{c}$ in $[c_*, c^*]$ all tend to zero as $a \rightarrow \frac{1}{2}^-$.

We suspect that a similar picture holds for the model of Faye, but it is not clear that our analysis is able to prove this much. The FitzHugh-Nagumo condition that $a - \frac{1}{2}$ is small would be replaced here by requiring that $\int_{u_0}^{u_+} (q_0 S(u) - u) du$ is small.

4.3. Model of Pinto and Ermentrout. We said in the introduction that there was only a partial existence result for the model in [16]. We were referring there to a recent paper by Faye and Scheel [5], which uses an interesting extension of the geometric perturbation method to infinite dimensional spaces to handle this kind

of problem. The method is powerful because it allows an extension beyond the sorts of kernel which reduce the problem to an ode.

Faye and Scheel remark that their paper appears to apply to the Pinto-Ermentrout model. This is true, but with a limitation. A key hypothesis in their paper is that for the singular solution, as described above, the jump down occurs above the knee. In a private communication Professor Ermentrout has observed that while this is true for the Pinto-Ermentrout model in some parameter ranges, it is also common for the down-jump to occur at the knee. This is why we characterized their result as "partial" for Pinto-Ermentrout.

Unfortunately, we have not been able to make our approach work for Pinto-Ermentrout. The reason may be related to an important difference between (2.1) and the equivalent set of ode's obtained from (1.5). The linearization of (2.1) around its equilibrium point has only real eigenvalues, for any $\varepsilon > 0$, while the equivalent linearization for (1.5) has complex eigenvalues for a range of positive ε . Thus, a homoclinic orbit would oscillate around equilibrium. A few oscillations could occur even for the very small values of ε where the eigenvalues are real. The final steps in our proof above clearly do not allow such oscillations.

In [[9]] we showed that there was co-existence of complex roots and a homoclinic orbit for FitzHugh-Nagumo, and observed that work of Evans, Fenichel and Feroe then implied the existence of many periodic solutions and a form of chaos. This leads to a conjecture that the Pinto-Ermentrout model supports a richer variety of bounded solutions than the model of Faye. The new solutions are probably unstable, however, so their physical importance is unclear.

4.4. Stability of these solutions. A local stability result for the fast solution was proved by Faye. His proof depends crucially on analysis of both the front and back of his solution, as described above. The analysis of the back is less standard because of the assumption that the jump down is at the knee. Here he relies on previous work on similar problems. Presumably if the jump were above the knee (where, however his existence proof is not claimed to apply), the stability analysis would be easier.

4.5. Can the hypotheses of Theorem 2 be checked rigorously for a specific (ε, c_1) ? Condition (i) says that the solution p_{ε, c_1} is on the unstable manifold $\mathcal{U}_{\varepsilon, c_1}^+$ of (2.1) at the equilibrium point p_0 . To check condition (ii) we must follow p_{ε, c_1} until a point where $u_{\varepsilon, c_1} = 0$. Our proposal for doing this is based on [7], where a similar procedure was followed for the well known equations of Lorenz.

Using a standard ode solver we can arrive at a conjectured value for (ε, c_1) . To begin analyzing p_{ε, c_1} numerically we would expand the solutions around p_0 . A high order expansion of $\mathcal{U}_{\varepsilon, c}^+$ results in algebraic expressions which are then evaluated using rigorous numerical analysis based on interval arithmetic. With this technique one hopes to show that $\mathcal{U}_{\varepsilon, c}^+$ enters a very small box near p_0 . For the example in [7] this box had a diameter of about 10^{-68} . This gives us an initial estimate accurate to (say) 68 significant digits.

From there, a rigorous ode solver, as described for example in [1], would be used to continue p_{ε, c_1} until $w_{\varepsilon, c_1} = 0$. Whether this can be done cannot be determined ahead of time. One has to run the solver. The number of guaranteed accurate digits decreases as the integration proceeds. We then hope that some significant

digits would be maintained long enough to reach $u = 0$. It must be checked along the way that $\max u_{\varepsilon, c_1} > u_{knee}$.

Based on the great sensitivity of the Lorenz equations to the initial conditions, we expect that this would be easier for the Faye model than it was in [7]. We are not aware of any proposal to try to estimate ε for the method of geometric perturbation.

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APPENDIX A. PROOFS OF LEMMAS 1, 2, AND 14.

A.1. Proofs of Lemma 1 and Lemma 2. We prove these results together. The linearization of (2.2) around $r_0 = (u_0, u_0, 0)$ is the system $Q' = AQ$ with

$$A = \begin{pmatrix} -\frac{1}{c} & \frac{1}{c} & 0 \\ 0 & 0 & 1 \\ -b^2 q_0 S'(u_0) & b^2 & 0 \end{pmatrix}.$$

The characteristic polynomial of A is

$$(A.1) \quad f(X) = X^3 + \frac{1}{c}X^2 - b^2X - \frac{b^2}{c}(1 - S'(u_0)q_0),$$

Recall that $h(u) = \frac{u}{S(u)}$. Condition 4 implies that the equation $q_0 = h(u)$ has three solutions, $u_0 < u_m < u_+$, and by Condition 2, $h'(u_0) > 0$. It follows that

$$(A.2) \quad q_0 S'(u_0) < 1.$$

Therefore $f(0) < 0$. Also, $f'(0) = -b^2$, and both f'' and f''' are positive for $X > 0$. Hence A has one real positive eigenvalue. Also, $f(-\frac{1}{c}) = \frac{b^2}{c} S'(u_0) q_0 > 0$, which implies that A has two real negative eigenvalues.

Further, it is easily seen that there is an eigenvector corresponding to the positive eigenvalue of A which points into the positive octant. If $r = (u, v, w)$ is a solution lying on the branch $\mathcal{U}_{0,c}^+$ of the unstable manifold of (2.2) at r_0 , then initially, u' , $v' = w$, and w' are positive. It follows from the first two equations of (2.2) that $v > u$ as long as $w > 0$. Also, $u \geq q_0 S(u)$ for $u_0 \leq u \leq u_m$ and so $w' > 0$ while u is in $(u_0, u_m]$. Hence there is a first t_0 such that $u(t_0) = u_m$, and we can assume that $t_0 = 0$. We have now proved the assertions of the first and second sentences of Lemma 1.

For the third sentence of Lemma 1, and for all of Lemma 2, we need a comparison lemma. For each $c > 0$, let $r_c = (u_c, v_c, w_c)$ be the unique solution of (2.2) on $\mathcal{U}_{0,c}^+$ such that $w_c > 0$ on $(-\infty, 0]$ and $u_c(0) = u_m$. Suppose that $w_c > 0$ on a maximal interval $(-\infty, T(c))$, where possibly $T(c) = \infty$. Then in $(-\infty, T(c))$ we can consider u and w as functions of v , letting $u_c(t) = U_c(v_c(t))$ and $w_c(t) = W_c(v_c(t))$. This defines the functions U_c and W_c on the interval

$$I_c = (u_0, \lim_{t \rightarrow T(c)^-} v_c(t)),$$

and for v in this interval,

$$(A.3) \quad U'_c(v) = \frac{v - U_c(v)}{cW_c(v)}, \quad W'_c(v) = \frac{b^2(v - q_0 S(U_c(v)))}{W_c(v)}.$$

Lemma 18. *If $d_2 > d_1 > 0$ then $I_{d_1} \subset I_{d_2}$. In the interval I_{d_1} ,*

$$(A.4) \quad \begin{aligned} U_{d_2} &< U_{d_1} \\ W_{d_2} &> W_{d_1} \end{aligned}.$$

Proof. The first sentence follows by proving (A.4) on the smaller of the two intervals. We first show that these inequalities hold on some initial interval $u_0 < v < u_0 + \delta$. This is seen by comparing unit eigenvectors corresponding to the positive eigenvalues $\lambda_1(d_1)$ and $\lambda_1(d_2)$ of the linearizations of (2.2) around r_0 . Suppose that for a particular c the eigenvector corresponding to $\lambda_1(c)$ is $(n_1(c), n_2(c), n_3(c))$. Then

$$\begin{aligned} n_1(c) &= \frac{n_2(c)}{(1 + \lambda_1(c))} \\ n_3(c) &= \lambda_1(c) n_2(c). \end{aligned}$$

Inequalities (A.4) follow near r_0 if $\lambda_1(d_2) > \lambda_1(d_1)$. For this we turn to the characteristic polynomial of A , given in (A.1) but now denoted by $f(X, c)$.

It is easier to work with $F = cf$, noting that $c > 0$. The positive eigenvalue of A is determined by the equation

$$F(\lambda_1(c), c) = 0$$

and the condition $\lambda_1(c) > 0$. Then

$$\frac{\partial F}{\partial X}(\lambda_1(c), c) \frac{d\lambda_1(c)}{dc} = -\frac{\partial F}{\partial c}(\lambda_1(c), c).$$

Since $F(0, c) < 0$, $\frac{\partial F}{\partial X}(0, c) < 0$ and $\frac{\partial^2 F}{\partial X^2}(X, c) > 0$ for $X \geq 0$, $\frac{\partial F}{\partial X}(\lambda_1(c), c) > 0$. Also, $\frac{\partial F}{\partial c}(\lambda_1, c) = \lambda_1(\lambda_1^2 - b^2)$. It follows that $\frac{d\lambda_1(c)}{dc} > 0$ if $\lambda_1 < b$. But

$$F(b, c) = \frac{b^2}{c} S'(u_0) q_0 > 0,$$

so indeed, $\lambda_1(c) < b$.

Therefore (A.4) holds on some interval $(u_0, u_0 + \delta)$. Suppose that the first inequality fails at a first $\hat{v} \in I_{d_1}$, while the second holds over $(u_0, \hat{v}]$. Then at \hat{v} , $U_1 = U_2$, $W_2 > W_1$. But then, $U_2'(\hat{v}) < U_1'(\hat{v})$, a contradiction since $U_2 < U_1$ on $(0, \hat{v}]$. A similar argument eliminates the other possibilities, using the fact that S is increasing, and this completes the proof of the Lemma 18. \square

Corollary 2. *If $T(d_1) = \infty$ then $T(d_2) = \infty$.*

Lemma 19. *If $d_2 \geq d_1$, $T(d_1) < \infty$, and $v_{d_1}(T(d_1)) > q_0 S(u_{knee})$, then either $T(d_2) = \infty$ or $u_{d_2}(T(d_2)) > u_{knee}$.*

Proof. Suppose that $T(d_2) < \infty$ and $u_{d_2}(T(d_2)) \leq u_{knee}$. Lemma 18 implies that $v_{d_2}(T(d_2)) \geq v_{d_1}(T(d_1))$ and so

$$w'_{d_2}(T(d_2)) = b^2(v_{d_2}(T(d_2)) - q_0 S(u_{d_2}(T(d_2)))) \geq b^2(v_{d_2}(T(d_2)) - q_0 S(u_{knee})) > 0,$$

a contradiction because $T(d_2)$ is the first zero of w_{d_2} . \square

Next we must show the existence of c_0^* .

Lemma 20. *For sufficiently large c , $T(c) = \infty$.*

Proof. From (A.3), in the interval $(-\infty, T(c))$, where v_c is increasing, $v_c > u_c$. Recall that

$$\frac{u}{S(u)} > q_0$$

in (u_0, u_m) . As long as $u_0 < U_c(v_c) < u_m$ and $v_c < 1$,

$$\frac{dU_c}{dW_c} = \frac{v - U_c}{cb^2 S(U_c) \left(\frac{v}{S(U_c)} - q_0 \right)} < \frac{1}{c\eta \left(\frac{U_c}{S(U_c)} - q_0 \right)}.$$

This implies that for large c , in the interval where $u_0 < u_c < u_m$, w_c grows rapidly and so, in turn, does v_c . In particular, $v_c > 1$ before $u_c = u_m$, and this implies that $T(c) = \infty$. \square

Now we wish to show that for small $c > 0$, $w_c < 0$ before $v_c = 1$. It is in this step that Condition 5 is used.

Lemma 21. *There is a $\bar{w} > 0$ such that for any $c > 0$, if $|w_c(\tau)| > \bar{w}$ and $0 < v_c(\tau) < 1$, then $|w_c| > \bar{w}$ for $t > \tau$ and v_c leaves the interval $(0, 1)$. If $w_c(\tau) > \bar{w}$ then v_c crosses 1, while if $w_c(\tau) < -\bar{w}$ then v_c crosses 0.*

Proof. Let $\bar{w} = \sqrt{2}b$. Since $|w'| \leq b^2$, if $w(\tau) = \sqrt{2}b$, then for $s > 0$, $w(\tau + s) \geq \sqrt{2}b - b^2 s$, from which follows that v must leave $(0, 1)$ before $s = \frac{\sqrt{2}}{b}$. \square

Lemma 22. *If $0 < w_c \leq \bar{w}$ on $(-\infty, \tau]$ then $0 < v_c - u_c < c\bar{w}$ on this interval. If $|w_c| \leq \bar{w}$ on $(-\infty, \sigma]$, then $|v_c - u_c| < c\bar{w}$ on this interval.*

Proof. With $r = r_c$, $(v - u)' = w - \frac{v-u}{c} \leq \bar{w} - \frac{v-u}{c}$, so if $v - u > c\bar{w}$ then $(v - u)' < 0$. Also, if $v - u = 0$ in $(-\infty, \tau)$ then $(v - u)' > 0$. Since $v - u \rightarrow 0^+$ as $t \rightarrow -\infty$, the first sentence of the lemma follows and the second is similar. \square

Based on this lemma, we consider, in addition to (2.2), the system

$$(A.5) \quad \begin{aligned} v' &= w \\ w' &= b^2(v - q_0 S(v)) \end{aligned} \quad ,$$

This system has equilibrium points at $(u_0, 0)$, $(u_m, 0)$, and $(u_+, 0)$, and a standard phase plane analysis, assuming Condition 5, shows that the positive branch $\mathcal{U}_{0,0}^+$ of unstable manifold of (A.5) at $(u_0, 0)$ is homoclinic. Also we consider the system

$$(A.6) \quad \begin{aligned} v' &= w \\ w' &= b^2(v - q_0 S(v - \hat{c})) \end{aligned} \quad ,$$

for small \hat{c} . Choose \hat{c} so small that this system also has three equilibrium points, and a homoclinic orbit based at the left most of these. This orbit entirely encloses the homoclinic orbit of (A.5).

Finally we consider the system

$$(A.7) \quad \begin{aligned} v' &= w \\ w' &= b^2(v - q_0 S(v + \hat{c})) \end{aligned} \quad ,$$

For sufficiently small \hat{c} this system also has a homoclinic orbit. This orbit lies entirely inside the homoclinic orbit of (A.5). However, the lower left branch $\mathcal{U}_{0,0}^-$ of the unstable manifold of this system crosses the homoclinic orbits of (A.5) and (A.6), and this branch will play a role below. (See Figure 12.)

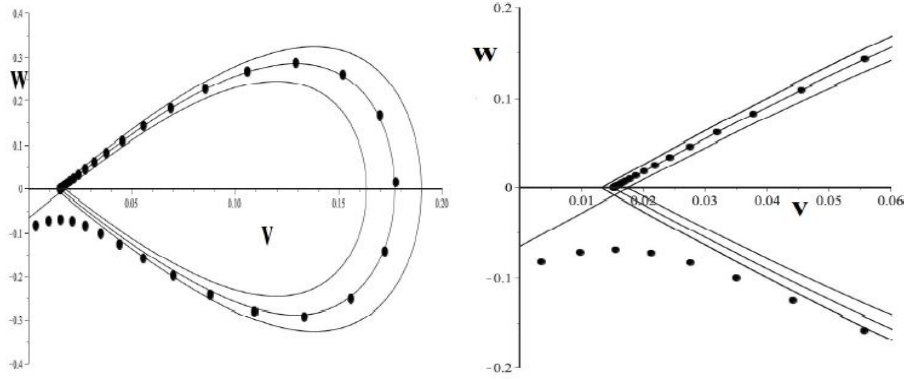


FIGURE 10. homoclinic orbits of, from inner to outer, (A.7), (A.5), and (A.6), part of $\mathcal{U}_{0,0}^-$ for (A.7), and an orbit of (2.2) (dotted)

From now on, (v_1, w_1) , (v_2, w_2) , and (v_3, w_3) will denote the unique solutions of the systems (A.5), (A.6), and (A.7) respectively which lie on the homoclinic orbits of those systems and satisfy $v_i(0) = u_m$. In each of these cases, if (v, w) is homoclinic then $|w|$ is bounded by \bar{w} . This follows from the definition of \bar{w} in Lemma 21, the results of which also apply to (A.6) and (A.7), with the same proofs. If $|w|$ exceeds \bar{w} then p is not bounded.

Recall that in Lemmas 1 and 2, $r_{0,c} = (u_{0,c}, v_{0,c}, w_{0,c})$ denoted the unique solution on the unstable manifold $\mathcal{U}_{0,c}$ such that $u_{0,c}(0) = u_m$ and $w_{0,c} > 0$ on $(-\infty, 0]$.

In the rest of this proof we will denote this solution by (u, v, w) . By Lemma 22 we can choose c so small that if t_1 is the first zero of w_c , then

$$(A.8) \quad v - \hat{c} < u < v$$

on $(-\infty, t_1]$.

Lemma 23. *Condition A.8 implies that if $w_c > 0$ on $(-\infty, t]$, then $(v_c(t), w_c(t))$ is in the annular region between the orbit of (v_1, w_1) and the orbit of (v_2, w_2) .*

Proof. The proof is similar to the proof of Lemma 18. As long as $w_c > 0$, u_c and w_c can be considered functions of v_c . Also,

$$(A.9) \quad \frac{dw_c}{dv_c} = \frac{b^2(v_c - q_0 S(u_c))}{w_c}.$$

By considering the eigenvalues of the linearizations of (A.5) as functions of c we can show, using (A.2), that for large negative t , $(v(t), w(t))$ lies in the claimed annular region. Suppose that for some first τ , $(v_c(\tau), w_c(\tau))$ lies on the upper boundary of this region, that is, on the homoclinic orbit of (A.6), at a point where $w > 0$. The slope of this homoclinic orbit at this point is

$$\frac{dw_2}{dv_2} = \frac{b^2(v_2 - q_0 S(v_2 - \hat{c}))}{w_2} = \frac{b^2(v_c(\tau) - q_0 S(v_c(\tau) - \hat{c}))}{w_c(\tau)}.$$

But $u_c(\tau) > v_c(\tau) - \hat{c}$ (since $u_c < v_c$ as long as $w_c \geq 0$), and since S is increasing and $w_c(\tau) > 0$, it follows from (A.9) that $\frac{dw_c}{dv_c} < \frac{dw_2}{dv_2}$, and so the curve (v_c, w_c) arrives at this point from outside of the annular region, contradicting the definition of τ . In a similar manner it is shown that (v_c, w_c) lies above the orbit of (v_1, w_1) as long as $w_c > 0$. This uses the bound $u_c < v_c$ as long as $w_c > 0$.

A similar comparison shows that if $t = t_1(c)$ is the first point where $w_c(t) = 0$ then $v_c(t_1(c))$ is an increasing function of c , for $0 < c < c_0^*$, and that for $c > c_0^*$, $w_c > 0$ on R . This shows the uniqueness of c_0^* . To complete the proof of Lemma 2 we show that from the first t_1 where $w_c(t_1) = 0$, the curve (v_c, w_c) lies either to the right or below the orbit (v_3, w_3) , and also below the left branch of the unstable manifold of (A.7), at least up to the point where $w_c = -\bar{w}$ ($= -\sqrt{2}b$). (If $w_c = -\bar{w}$, then, as in Lemma 21, v_c becomes negative, which is what we are trying to show. See Figure 8.) This follows by the same sort of comparison as above, now comparing (v_c, w_c) with the lower half of the unstable manifold of (A.7). This is possible because by Lemma 22, $u_c < v_c + \hat{c}$ as long as $-\bar{w} < w_c < 0$.

To prove that c_0^* as defined in Lemma 2 exists, we note that the set of c such that $w(s_1) < 0$ for some s_1 is open, as is the set of c such that $v(s_2) > 1$ for some s_2 and $v > 0$ on $(-\infty, s_2]$. This follows because p_c is a continuous function of c . Lemmas 20 and 23 imply that these sets are nonempty, and their definitions and Proposition 1 imply that they are disjoint. Since the interval $(0, \infty)$ is connected, the existence of some positive c_0^* which is not in either set. Its uniqueness follows from the Corollary to Lemma 12.

From the definition of c_0^* , $w_{c_0^*} \geq 0$ on R . Suppose that there is an s with $w_{c_0^*}(s) = 0$ and $w_{c_0^*}(t) > 0$ on $(-\infty, s)$. Then $w'_{c_0^*}(s) = 0$, $w''_{c_0^*}(s) \geq 0$ and

$$w''_{c_0^*}(s) = -b^2 q_0 S'(u_{c_0^*}(s)) u'_{c_0^*}(s).$$

Because $v'_{c_0^*} > 0$ on $(-\infty, s)$, $u'_{c_0^*}(s) > 0$, giving $w''_{c_0^*}(s) < 0$. This contradiction completes the proof of Lemma 1. \square

To complete Lemma 2 we must prove the assertions in the third and fourth sentences. In the third sentence,

$$u'' = \frac{v' - u'}{c} = \frac{w}{c}$$

when $u' = 0$, and at the first zero of u' , $w < 0$, so $u'' < 0$. The implicit function theorem and the comparison (A.4) imply the limit statement.

For the last sentence of Lemma 2, it suffices to prove that $u_{0,c}(T(c)) > u_{knee}$. Suppose instead that $u_{0,c}(T(c)) \leq u_{knee}$. Since $c \geq c_1$, Lemma 18 and the hypotheses of Lemma 2 imply that

$$\begin{aligned} v_{0,c}(T(c)) &> v_{0,c_1}(T(c_1)) > q_0 S(u_{knee}) \\ &\geq q_0 S(u_{0,c}(T(c))). \end{aligned}$$

Hence $w'(T(c)) > 0$, which contradicts the definition of $T(c)$. This completes the proof of Lemma 2.

A.2. Proof of Lemma 14.

Proof. This result is about system (2.1). However the argument in Lemma 21, initially about system (2.2), applies equally well to (2.1), so if w_c increases monotonically to above \bar{w} then v crosses 1, followed by u . Hence we can assume that if s_1 is the first zero, if any, of w_c , then $w_c < \bar{w}$ on $(0, s_1)$. As earlier in obtaining (A.8), it follows that if $p = p_c$, then

$$(A.10) \quad v > u > v - c\bar{w}$$

on $(0, s_1)$. Therefore,

$$(A.11) \quad \lim_{c \rightarrow 0^+} (u - v) = 0$$

uniformly on $(0, s_1]$ and for $\varepsilon > 0$.

Also,

$$(A.12) \quad \lim_{\varepsilon \rightarrow \infty} \left(q - \frac{1}{1 + \beta S(u)} \right) = 0,$$

uniformly on $(-\infty, s_1]$ and for $c > 0$, $\varepsilon > 0$. This is proved by the same argument which lead to (A.11), .

Now consider the equation obtained from (2.1) by formally setting $c = 0$ in (2.1), namely

$$(A.13) \quad v'' = b^2 Z(v),$$

where

$$Z(v) = v - \frac{S(v)}{1 + \beta S(v)}.$$

Because (2.1) has only one equilibrium point, $Z(v) > 0$ if $v > 0$. Hence there is a $\hat{t} > 0$ such that if for some t , $u_m \leq v(t) < 1$ and $v'(t) > 0$, then $v(t + \hat{t}) > 1$. (Here \hat{t} is independent of the particular solution involved.) Lemma 14 then follows from (A.11) and (A.12). \square

APPENDIX B. PROOF OF LEMMA 3

Proof. Suppose that the linearization of (2.1) around p_0 is $P' = BP$. Then

$$(B.1) \quad B = \begin{pmatrix} -\frac{1}{c} & \frac{1}{c} & 0 & 0 \\ 0 & 0 & 1 & 0 \\ -b^2 q_0 S'(u_0) & b^2 & 0 & -b^2 S(u_0) \\ -\frac{\varepsilon}{c} \beta q_0 S'(u_0) & 0 & 0 & -\frac{\varepsilon}{c} (1 + \beta S(u_0)) \end{pmatrix}.$$

The characteristic polynomial of B is

$$(B.2) \quad g(X) = X^4 + \frac{1}{c} (1 + \varepsilon (\beta S(u_0) + 1)) X^3 + \left(-b^2 + \frac{1}{c^2} \varepsilon (\beta S(u_0) + 1) \right) X^2 \\ + \frac{b^2}{c} (q_0 S'(u_0) - 1 - \varepsilon (\beta S(u_0) + 1)) X \\ + \frac{b^2}{c^2} \varepsilon (q_0 S'(u_0) - 1 - \beta S(u_0))$$

While proving Lemma 1 we showed that if $\varepsilon = 0$, then one of the non-zero eigenvalues of B is positive and two are real and negative. We also saw that $q_0 S'(u_0) < 1$, and therefore, $\det B < 0$ if $\varepsilon > 0$. Since the trace of B is also negative, if $\varepsilon > 0$ then B has either one or three eigenvalues with negative real part, and for sufficiently small $\frac{\varepsilon}{c}$ it has three, all of which are real. In fact, since $g(0) < 0$, $g'(0) < 0$, and $g'''(X) > 0$ if $X > 0$, B has exactly one real positive eigenvalue for every (ε, c) in the positive quadrant $\varepsilon > 0, c > 0$. For each $c > 0$, as ε increases the other roots of g remain in the left hand plane unless, for some ε , two of them are pure imaginary. Consideration of the characteristic polynomial in this case (one negative, one positive, and two pure imaginary roots) shows that the coefficients of X and X^3 have the same sign. This is not the case with g , because the coefficient of X^3 is positive and the coefficient of X is negative.

Hence, as asserted in Lemma 3, the unstable manifold $\mathcal{U}_{\varepsilon, c}$ of (2.1) at p_0 is one dimensional. Further, because $q_0 S'(u_0) < 1$, it follows from (B.1) that if $\mu = (\mu_1, \mu_2, \mu_3, \mu_4)$ is the unit eigenvector of B with $\mu_1 > 0$, then $\mu_2 > 0$, and $\mu_3 > 0$. Also (B.1) implies that if $\varepsilon = 0$ then $\mu_4 = 0$ and if $\varepsilon > 0$ then $\mu_4 < 0$. The claimed behavior for large negative t of solutions on $\mathcal{U}_{\varepsilon, c}$ follows. The continuity of $\mathcal{U}_{\varepsilon, c}$ for $\varepsilon \geq 0$ follows from Theorem 6.1 in chapter 6 in the text of Hartman, [11].⁹

The final assertion of the lemma, that $\lambda_1(c, \varepsilon) > \lambda_1(c, 0)$ if $c > 0$ and $\varepsilon > 0$ follows by writing the characteristic polynomial of B in the form

$$g(x) = X f(X) + \frac{\varepsilon}{c} (1 + \beta S(u_0)) f(X) - \frac{\varepsilon}{c} b^2 S(u_0) \beta S'(u_0) q_0.$$

We see that since $f(\lambda_1(c, 0)) = 0$, $g(\lambda_1(c, 0)) < 0$. Hence $\lambda_1(c, \varepsilon) > \lambda_1(c, 0)$, completing the proof of Lemma 3. \square

⁹Our terminology is different from Hartman's because we define stable and unstable manifolds even when $\varepsilon = 0$. In this case the unstable manifold $\mathcal{U}_{\varepsilon, c}^+$, all we need, is the set of all solutions $p(t)$ which tend to p_0 at an exponential rate as $t \rightarrow -\infty$. To obtain the desired continuity of $\mathcal{U}_{\varepsilon, c}^+$ with respect to ε and c , apply Hartman's theorem to (2.2) augmented with equations $\varepsilon' = 0$ and $c' = 0$. This is the closest we come to center manifolds in our approach.